Asian Herpetological Research 2019, 10(1): 1–12
DOI: 10.16373/j.cnki.ahr.180058

ORIGINAL ARTICLE

Resurrection of the Genus *Leptomantis*, with Description of a New Genus to the Family Rhacophoridae (Amphibia: Anura)

Dechun JIANG[1], Ke JIANG[1], Jinlong REN[1,2], Jun WU[3] and Jiatang LI[1,4,5*]

[1] *CAS Key Laboratory of Mountain Ecological Restoration and Bioresource Utilization & Ecological Restoration and Biodiversity Conservation Key Laboratory of Sichuan Province*, *Chengdu Institute of Biology*, *Chinese Academy of Sciences*, *Chengdu* 610041, *Sichuan*, *China*
[2] *University of Chinese Academy of Sciences*, *Beijing* 100049, *China*
[3] *Nanjing Institute of Environmental Sciences*, *Ministry of Ecology and Environment of China*, *Nanjing* 210042, *Jiangsu*, *China*
[4] *CAS Center for Excellence in Animal Evolution and Genetics*, *Chinese Academy of Sciences*, *Kunming* 650223, *Yunnan*, *China*
[5] *Southeast Asia Biodiversity Research Institute*, *Chinese Academy of Sciences*, *Yezin Nay Pyi Taw* 05282, *Myanmar*

Abstract Genus *Rhacophorus* Kuhl and Van Hasselt, 1 822 is one of the most diverse genera of the family Rhacophoridae, and its taxonomy of genus *Rhacophorus* faces major challenges because of rapidly described new species and complex interspecies relations. In this study, we investigate the generic taxonomy within the genus *Rhacophorus* based on 1 972 bp of mitochondrial genes (12S rRNA, tRNA-val and 16S rRNA), containing 102 sequences from 58 species. The results reveal three well-supported and highly diverged matrilines that correspond with morphological characteristics and geographic distribution. Accordingly, we consider these three lineages as distinct genera: *Rhacophorus sensu stricto*, resurrected genus *Leptomantis* Peters, 1867, and the genus *Zhangixalus* **gen. nov.**

Keywords *Rhacophorus*, taxonomic revision, tree frog, *Zhangixalus* **gen. nov.**

1. Introduction

Old World Treefrogs, family Rhacophoridae, comprise 416 species in 18 recognized genera (Frost, 2018), of which 78 species in 12 genera are found in southern and southwestern China (AmphibiaChina, 2018). Of these, genus *Rhacophorus* Kuhl and Van Hassalt, 1 822 contains 92 species, distributed widely across China, Japan, India, and from the Philippines to Sulawesi (Frost, 2018; O'Connell *et al*., 2018). Genus *Leptomantis* Peters, 1867 was established for the species *L. bimaculata* Peters, 1867, and Ahl (1931) subsequently synonymized it as a junior synonym of *Rhacophorus*. Later, Dubois (1987) made *Leptomantis* a subgenus of *Rhacophorus*, and divided subgenus *Rhacophorus* into ten species groups. Iskandar and Colijn (2000) subsequently raised *Leptomantis* to full genus rank, but Harvey *et al.* (2002) again synonymized *Leptomantis* with *Rhacophorus*, which Frost (2018) accepted. Fei (2012) established *Huangixalus* based on the type species *Rhacophorus translineatus* Wu, 1977, but treated as synonym of *Rhacophorus* by Frost (2018).

Recently, many new species of the genus *Rhacophorus* were revealed by virtue of molecular phylogenetic results (Matsui *et al*., 2013; Nguyen *et al*., 2017; Streicher *et al*., 2014). In addition, several phylogenetic works have shed new light on the generic phylogeny of *Rhacophorus*, which constantly recovered as three well-supported lineages on the basis of molecular phylogenetic trees, although their phylogenetic relationships remain unresolved (Chan *et al*., 2018; Li *et al*., 2008, 2009, 2012, 2013; O'Connell *et al*., 2018; Pan *et al*., 2017).

* Corresponding author: Prof. Jiatang LI, from Chengdu Institute of Biology, Chinese Academy of Sciences, China, with his research focusing on molecular phylogeny, systematics, biogeography, and evolution of amphibians and reptiles.
E-mail: lijt@cib.ac.cn
Received: 7 August 2018 Accepted: 10 March 2019

The three major clades show deep divergence with each other. The morphological characteristics of tree frog species within their respective clades differ substantially (Li *et al*., 2012; Yang, 2018). A clade that contains species from the Malay Peninsula to the Philippines agrees with the diagnosis of *Leptomantis*. On the basis of molecular phylogenetic results, morphological comparisons and distribution patterns, we recognize the validity of the genus *Leptomantis*. Additionally, resolved relationships require the further splitting of *Rhacophorus* and the erection of a new genus.

2. Material and Methods

2.1. Morphological characters and distribution collection Morphological characters used and their measurement methods followed Fei *et al*. (2009), morphological characters used as below: body size, snout-vent length (SVL); dermal folds along limbs, dermal folds or ridges along outer edge of forearm and tarsus; supracloacal fold, skin folds above cloaca; tarsal projection, a dermal projection on tibiotarsal articulation; upper eyelid projection, conical projection on upper eyelid. Morphological data of genera were obtained from previous studies (Abraham *et al*., 2013; Biju *et al*., 2010; Boulenger, 1882; Dubois, 1987; Fei *et al*., 2009; Jiang *et al*., 2016; Peters, 1867). The morphological descriptions, phylogentic assignments, and distributions of species of *Rhacophorus* were based on original descriptions and the following subsequent literature: Anderson (1871), Biju *et al*. (2013), Boulenger (1896), Das and Haas (2005), Dehling (2008; 2015), Dehling and Grafe (2008), Hamidy and Kurniati (2015), Harvey *et al*. (2002), Hertwig *et al*. (2012), Inger (1954; 1966; 1999), Li *et al*. (2012), Malkmus and Brühl (2002), Matsui and Panha (2006), Matsui *et al*. (2013), Mo *et al*. (2008), Nguyen *et al*. (2017), Ohler and Delorme (2006), Onn and Ahmad (2009), Orlov *et al*. (2001, 2008, 2010, 2012), Ostroshabov *et al*. (2013), Rowley *et al*. (2012), and Streicher *et al*. (2014).

2.2. Phylogenetic analyses We downloaded 102 sequences for 55 species of *Rhacophorus* and three outgroups from GenBank. *Chiromantis xerampelina* Peters, 1854, *Polypedates megacephalus* Hallowell, 1861 and *Polypedates leucomystax* (Gravenhorst, 1829) were selected as outgroups for phylogenetic analyses (Li *et al*., 2008, 2009). The respective gene partitions were 12S rRNA, tRNA-val and 16S rRNA (1 972 bp alignment totally). Details on specimen voucher, GenBank accession codes and sampling sites were listed in Table S1.

The mitochondrial gene fragments were aligned by using the FasParser software package (Sun, 2017). After initial comparison, we partitioned the data sets and assigned substitution models as suggested by the Bayesian Information Criterion (BIC) as calculated in PartitionFinder v2.1.1 (Lanfear *et al*., 2012). This resulted in one partition for the data set with a GTR+I+G substitution model. The Bayesian phylogenetic relationships were conducted using MrBayes v3.2.6 (Ronquist *et al*., 2012). Two independent runs of Markov Chains for 10 000 000 generations were summarized, and sampled every 100 generations. The first 25 000 sampled trees were discarded as a conservative burn-in and convergence was investigated in Tracer v1.6 (Rambaut *et al*., 2013). The frequency of nodal resolution, termed a Bayesian posterior probability (BPP), was determined to assess confidence of the topology. Nodes were considered strongly supported when BPP $\geq$ 0.95. A maximum likelihood (ML) tree was conducted with RAxML v8.0.17 (Stamatakis, 2006) using a GTR+I+G model for our final likelihood search during fast bootstrapping with 1000 pseudoreplicates, bootstrap proportions (BSP) were assessed to test the node support, where nodes with BSP $\geq$ 70 were supported significantly. The alignment was partitioned for each locus.

3. Results

The two phylogenetic methods (BI, ML) resolved each major clade with strong support (Figure 1; Figure S1). The genus *Rhacophorus* was recovered to be a monophyletic group with strong support (BPP = 1.00; BSP = 100); *Rhacophorus* contained three strongly supported clades (Clades A, B, C), that were highly diverged with long basal branch lengths. Detailed content of these clades as follows: Clade A contained the following species: *R. orlovi* Ziegler and Köhler, 2001; *R. calcaneus* Smith, 1924; *R. verrucopus* Huang, 1983; *R. robertingeri* Orlov, Poyarkov, Vassilieva, Ananjeva, Nguyen, Sang, and Geissler, 2012; *R. translineatus* Wu, 1977; *R. annamensis* Smith, 1924; *R. exechopygus* Inger, Orlov, and Darevsky, 1999; *R. baluensis* Inger, 1954; *R. rhodopus* Liu and Hu, 1960; *R. reinwardtii* (Schlegel, 1840); *R. norhayatii* Chan and Grismer, 2010; *R. borneensis* Matsui, Shimada, and Sudin, 2013; *R. bipunctatus* Ahl, 1927; *R. kio* Ohler and Delorme, 2006; *R. helenae* Rowley, Tran, Hoang, and Le, 2012; *R. pardalis* Günther, 1858; *R. malabaricus* Jerdon, 1870; *R. pseudomalabaricus* Vasudevan and Dutta, 2000; *R. lateralis* Boulenger, 1883; *R. nigropalmatus* Boulenger, 1895; *R. bengkuluensis* Streicher, Hamidy, Harvey, Anders, Shaney, Kurniawan, and Smith, 2014; *R. margaritifer*

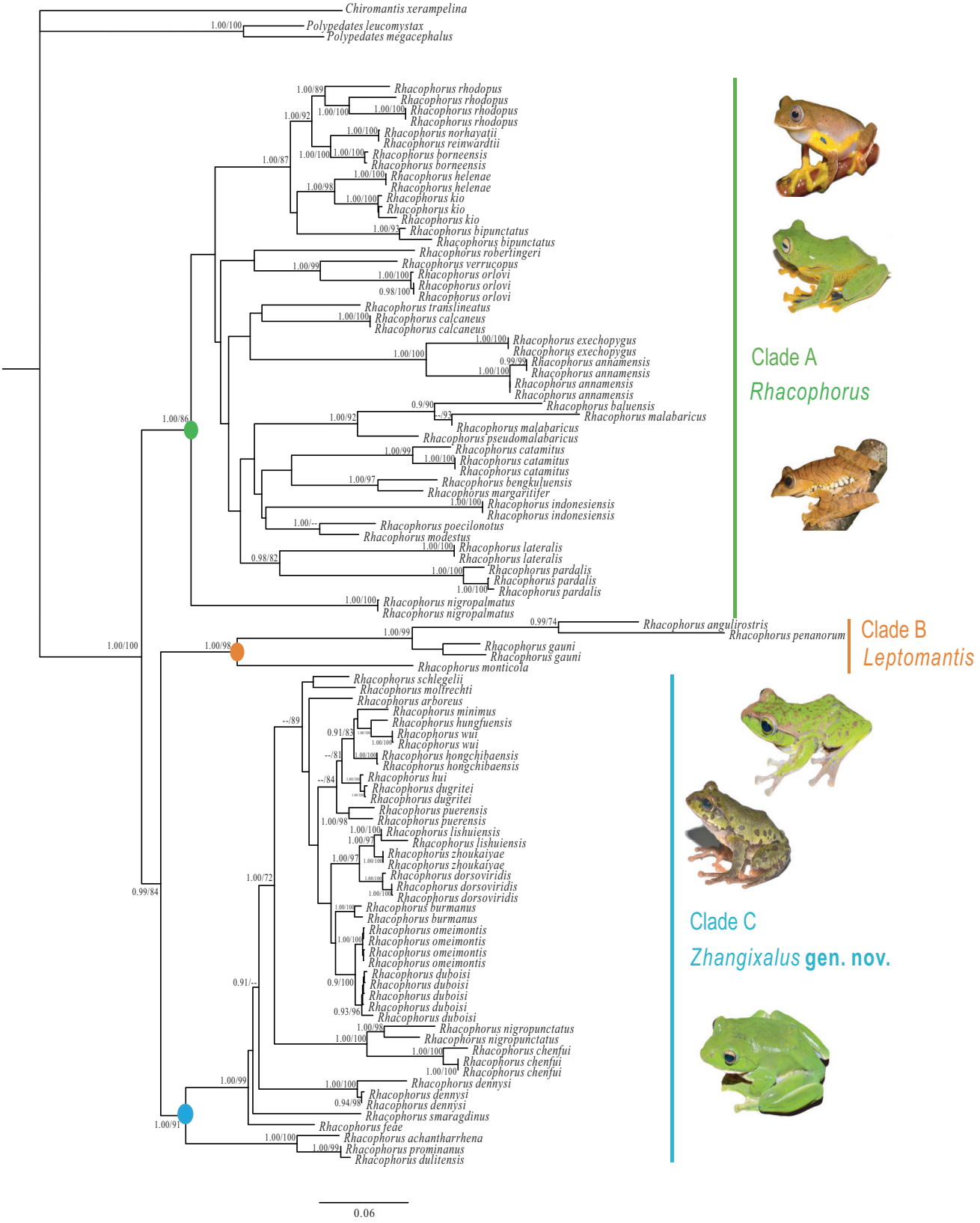

Figure 1 Phylogenetic relationships of species of *Rhacophorus* based on three mitochondrial genes: 12S rRNA, tRNA-val and 16S rRNA. Circles on nodes correspond to three clades: Clade A (green), Clade B (orange), Clade C (blue). Numbers beside the nodes are given as Bayesian posterior probabilities (BPP) (≥0.90 retained)/bootstrap proportions (BSP) for maximum likelihood analyses (≥70 retained); '--' represents BPP and BSP lower than 90% and 70, respectively. Photos were taken by Ke JIANG, Cheng LI, Jin-Long REN.

(Schlegel, 1837); *R. modestus* Boulenger, 1920; *R. poecilonotus* Boulenger, 1920; *R. indonesiensis* Hamidy and Kurniati, 2015; *R. catamitus* Harvey, Pemberton, and Smith, 2002 (BPP = 1.00). Among them, *R. rhodopus* from four areas (Longchuan, Lvchun, Mengyang and Medog) formed a well-supported lineage (BPP = 1.00; BSP = 86). *Rhacophorus kio* from Yunnan, China and Vietnam formed a lineage, which was sister to *R. helenae* from southern Vietnam (BPP = 1.00; BSP = 98).

Clade B contained the following species: *R. gauni* (Inger, 1966); *R. penanorum* Dehling, 2008; *R. angulirostris* Ahl, 1927; and *R. monticola* Boulenger, 1896 (BPP = 1.00; BSP = 98). This clade had species widely distributed in maritime Southeast Asia, from Peninsular Malaysia to the Philippines.

Clade C contained the following species: *R. feae* Boulenger, 1893; *R. moltrechti* Boulenger, 1908; *R. duboisi* Ohler, Marquis, Swan, and Grosjean, 2000; *R. omeimontis* (Stejneger, 1924); *R. burmanus* (Andersson, 1939); *R. dorsoviridis* Bourret, 1937; *R. zhoukaiyae* Pan, Zhang, and Zhang, 2017; *R. lishuiensis* Liu, Wang, and Jiang, 2017; *R. hui* Liu, 1945; *R. dugritei* (David, 1872); *R. hungfuensis* Liu and Hu, 1961; *R. wui* Li, Liu, Chen, Wu, Murphy, Zhao, Wang, and Zhang, 2012; *R. minimus* Rao, Wilkinson, and Liu, 2006; *R. hongchibaensis* Li, Liu, Chen, Wu, Murphy, Zhao, Wang, and Zhang, 2012; *R. puerensis* (He, 1999); *R. schlegelii* (Günther, 1858); *R. arboreus* (Okada and Kawano, 1924); *R. chenfui* Liu, 1945; *R. nigropunctatus* Liu, Hu, and Yang, 1962; *R. dennysi* Blanford, 1881; *R. smaragdinus* (Blyth, 1852); *R. dulitensis* Boulenger, 1892; *R. prominanus* Smith, 1924; and *R. achantharrhena* Harvey, Pemberton, and Smith, 2002 (BPP= 1.00). *Rhacophorus zhoukaiyae* from Anhui, China and *R. lishuiensis* from Zhejiang, China, formed a well-supported lineage (BPP = 1.00). Previous studies resolved *R. dorsoviridis* as the sister-species of *R. zhoukaiyae* (Pan *et al.*, 2017), and also was the sister-species of *R. lishuiensis* (Liu *et al.*, 2017). Because our data set included both *R. lishuiensis* and *R. zhoukaiyae*, the result indicated that *R. lishuiensis* had closer relationship with *R. zhoukaiyae* than *R. dorsoviridis* (BPP = 1.00; BSP = 97).

Distinct morphological differences diagnosed the three clades, including body sizes, dermal folds along limbs, tarsal projections, and dorsal coloration (Table 1). Further, differences in distribution among three clades were also obtained. Although Clade A covered all of Southeast Asia, clades B and C were rather isolated (Figure 2).

4. Discussion

Previous studies shed light on the phylogenetic resolution and systematics of Asian tree frogs. The molecular phylogeny of family Rhacophoridae resolved a monophyletic *Rhacophorus* and generally with three major clades (Chan *et al*., 2018; Li *et al.*, 2008, 2009, 2013). Several studies obtained species delimitations in *Rhacophorus* and all results showed a topology of three clades (Li *et al.*, 2012; O'Connell *et al*., 2018; Pan *et al*., 2017). However, the BPP values of root lineages remained low, which suggested uncertain phylogenetic relationships among these three clades. The genus

Table 1 Comparisons of morphology, distribution patterns, and reproduction models among the genera, *Rhacophorus*, *Leptomantis*, and *Zhangixalus* **gen. nov.**

	Rhacophorus	*Leptomantis*	*Zhangixalus* **gen. nov.**
Body size	moderate or large	relatively small	moderate or large
	SVL 30–100 mm, mostly above 40 mm	SVL 30–80 mm, mostly within 30–50 mm	SVL 30–120 mm, mostly above 50 mm
Dermal folds along limbs	present	absent	absent
Supracloacal fold	present or not	week or absent	absent
Tarsal projections	present	present or not	absent
Upper eyelid projection	absent	present or not	absent
Dorsal coloration	variable	light tan or reddish brown	mostly green
Distribution	across Southeast Asia	Maritime Southeast Asia	eastern Asia and northern Indochina
Reproduction models	foam nests or jelly-encapsuled eggs	foam nests	foam nests
Distribution	across Southeast Asia	Maritime Southeast Asia	eastern Asia and northern Indochina
Reproduction models	foam nests or jelly-encapsuled eggs	foam nests	foam nests

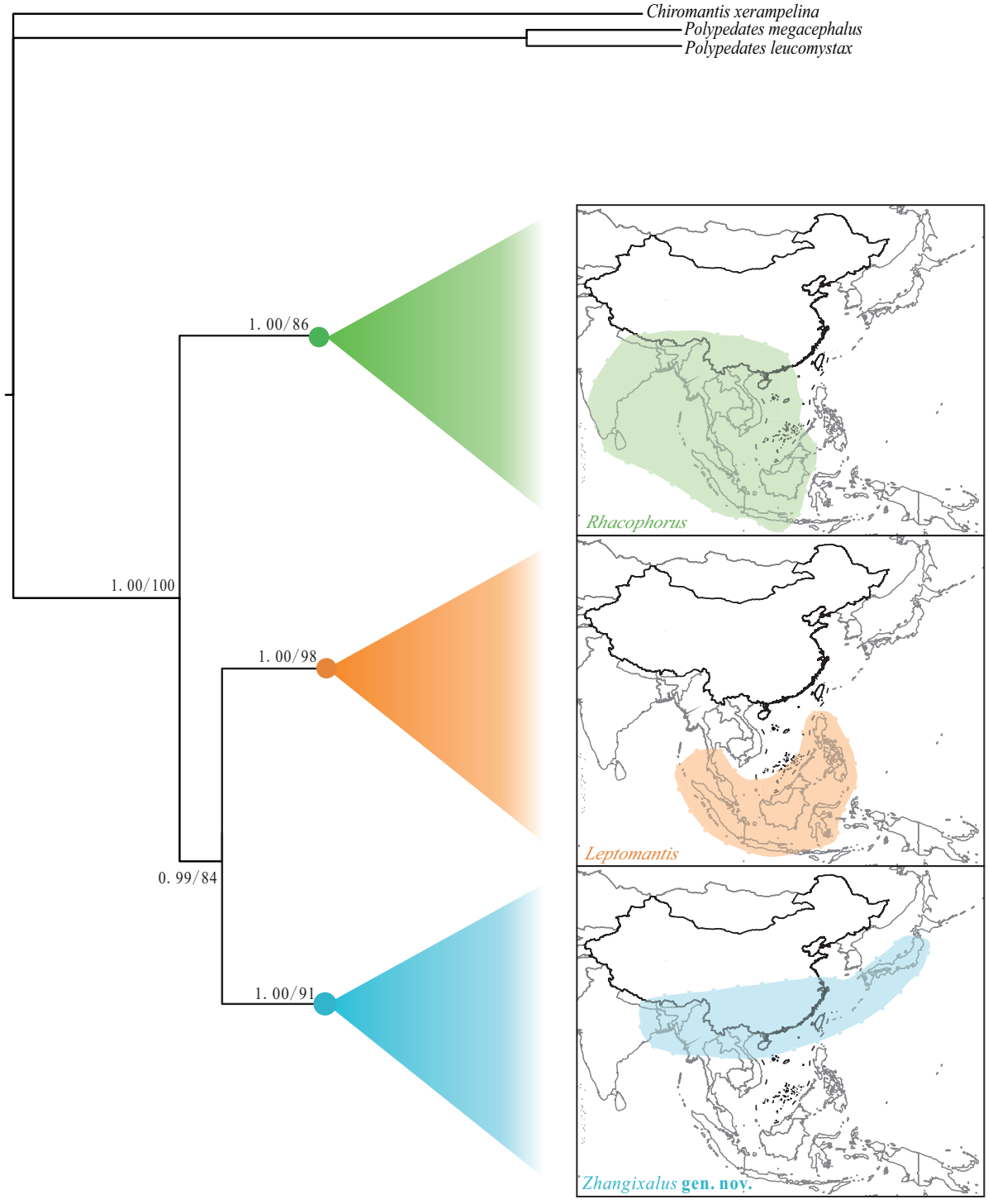

Figure 2 Comparison of distributions among three clades. Circles on nodes correspond to three clades: *Rhacophorus* (green), *Leptomantis* (orange), *Zhangixalus* **gen. nov.** (blue).

Leptomantis was established by Peters (1867) but its taxonomic status has long not been evaluated until now.

Our interpretations of *Rhacophorus* focus mainly on support values of root lineages. The molecular phylogeny depicts three well-supported matrilines, and these are consistent with the results of Li *et al.* (2012), although phylogenetic relationships of three clade differ. On the basis of highly supported molecular trees, distinct differences of morphological characteristics, and mostly non-overlapping geographic distribution, it is evident that these three

lineages show deep evolutionary divergences. Therefore, in order to better reflect the phylogenetic relationships and biogeographic history of these frogs, we propose to recognize each of the three lineages as a distinct genus: Clade A represents genus *Rhacophorus sensu stricto*; Clade B is valid genus *Leptomantis*, which consistent with the results of Iskandar and Colijn (2000); and Clade C requires erection of a new genus that we name here. Combined with this study and previous literature as shown before, we currently recognized 39 species in *Rhacophorus sensu stricto*, 14 species in *Leptomantis*, and 36 species in the new genus, respectively.

Taxonomic account

***Rhacophorus* Kuhl and Van Hasselt, 1822**

Type species: *Rhacophorus reinwardtii* (Schlegel, 1840)

Diagnosis: (1) Body size relatively moderate or large (SVL 30–100 mm, above 40 mm in most species); (2) presence of intercalary cartilage between terminal and penultimate phalanges of digits; (3) terminal phalanges of finger and toes Y-shaped; (4) tip of the digits expanded into large disks bearing circummarginal grooves; (5) webbed fingers; (6) skin not co-ossified to skull; (7) upper eyelid projections absent, tarsal projections present in most species; (8) dermal folds along forearm or tarsus present; (9) pupil horizontal; (10) iris without "X" shaped pattern; (11) white foam nests or jelly-encapsulated eggs produced by breeding pairs; and (12) distributed mainly in Indochina.

Phylogenetic definition: Genus *Rhacophorus* includes species that share a more recent common ancestor with *Rhacophorus reinwardtii* than with *Leptomantis bimaculata* and *Zhangixalus dugritei*.

Etymology: The generic name presumably derived from the Greek noon *rhakos*, meaning rag or tatter and the suffix-*phorus*, meaning bearer. The English common name of the genus is "Flying Frogs" or "Parachuting Frogs", and we suggest the Chinese name "Shu Wa Shu (树蛙属)". The gender of this genus is masculine.

Content: We currently recognized 39 species in the genus *Rhacophorus* as follows: *R. annamensis* Smith, 1924; *R. baluensis* Inger, 1954; *R. barisani* Harvey, Pemberton, and Smith, 2002; *R. bengkuluensis* Streicher, Hamidy, Harvey, Anders, Shaney, Kurniawan, and Smith, 2014; *R. bifasciatus* Van Kampen, 1923; *R. bipunctatus* Ahl, 1927; *R. borneensis* Matsui, Shimada, and Sudin, 2013; *R. calcadensis* Ahl, 1927; *R. calcaneus* Smith, 1924; *R. catamitus* Harvey, Pemberton, and Smith, 2002; *R. exechopygus* Inger, Orlov, and Darevsky, 1999; *R. helenae* Rowley, Tran, Hoang, and Le, 2012; *R. hoabinhensis* Nguyen, Pham, Nguyen, Ninh, and Ziegler, 2017; *R. hoanglienensis* Orlov, Lathrop, Murphy, and Ho, 2001; *R. indonesiensis* Hamidy and Kurniati, 2015; *R. kio* Ohler and Delorme, 2006; *R. laoshan* Mo, Jiang, Xie, and Ohler, 2008; *R. larissae* Ostroshabov, Orlov, and Nguyen, 2013; *R. lateralis* Boulenger, 1883; *R. malabaricus* Jerdon, 1870; *R. margaritifer* (Schlegel, 1837); *R. marmoridorsum* Orlov, 2008; *R. modestus* Boulenger, 1920; *R. nigropalmatus* Boulenger, 1895; *R. norhayatii* Chan and Grismer, 2010; *R. orlovi* Ziegler and Köhler, 2001; *R. pardalis* Günther, 1858; *R. poecilonotus* Boulenger, 1920; *R. pseudomalabaricus* Vasudevan and Dutta, 2000; *R. reinwardtii*; *R. rhodopus* Liu and Hu, 1960; *R. robertingeri* Orlov, Poyarkov, Vassilieva, Ananjeva, Nguyen, Sang, and Geissler, 2012; *R. spelaeus* Orlov, Gnophanxay, Phimminith, and Phomphoumy, 2010; *R. subansiriensis* Mathew and Sen, 2009; *R. translineatus* Wu, 1977; *R. tuberculatus* (Anderson, 1871); *R. vampyrus* Rowley, Le, Thi, Stuart, and Hoang, 2010; *R. verrucopus* Huang, 1983; and *R. viridimaculatus* Ostroshabov, Orlov, and Nguyen, 2013.

Distribution: Distributed widely across Southeast Asia, including India, Bangladesh, Vietnam, Laos, Thailand, Cambodia, Malaysia, Indonesia, and Brunei, as well as extreme southern and southwestern China (mainly in Hainan, Guangxi Zhuang Autonomous Region, Yunnan, and Tibetan Autonomous Region).

***Leptomantis* Peters, 1867**

Type species: *Leptomantis bimaculata* Peters, 1867

Diagnosis: (1) Body size relatively small (SVL 30–80 mm, about 30–50 mm in most species); (2) snout pointed or obtusely pointed; (3) terminal phalanges of finger and toes Y-shaped; (4) snout projections absent, upper eyelid projections present or not, tarsal projections absent in most species; (5) dermal folds along forearm or tarsus absent; (6) skin of dorsal surfaces smooth or finely shagreened; (7) webbed fingers; (8) dorsal coloration usually light tan or reddish brown; (9) iris without "X" shaped pattern; (10) white foam nests produced by breeding pairs; and (11) distributed in maritime Southeast Asia.

Phylogenetic definition: *Leptomantis* includes species that share a more recent common ancestor with *Leptomantis bimaculata* than with *Zhangixalus dugritei* and *Rhacophorus reinwardtii*.

Etymology: The generic name derived from the Greek adjective *leptos*, meaning thin or small and Greek noun *mantis*, meaning treefrogs. We suggest the English common name of the genus to be "Slim Treefrogs", and "Shou Shu Wa Shu (瘦树蛙属)" in Chinese. The gender of this genus is masculine.

Content: We currently recognized 14 species in the genus *Leptomantis* as follows: *L. angulirostris* (Ahl, 1927); *L. belalongensis* (Dehling and Grafe, 2008); *L. bimaculatus*

Peters, 1867; *L. cyanopunctatus* (Manthey and Steiof, 1998); *L. fasciatus* (Boulenger, 1895); *L. gadingensis* (Das and Haas, 2005); *L. gauni* (Inger, 1966); *L. harrissoni* (Inger and Haile, 1959); *L. malkmusi* (Dehling, 2015); *L. monticola* (Boulenger, 1896); *L. penanorum* (Dehling, 2008); *L. pseudacutirostris* (Dehling, 2011); and *L. robinsonii* (Boulenger, 1903); *L. rufipes* (Inger, 1966).

Distribution: Mainly maritime Southeast Asia, Malaysia, Singapore, Brunei, Indonesia, The Philippines, and southern Thailand.

***Zhangixalus* gen. nov. Li, Jiang, Ren, Jiang**

Type species: *Polypedates dugritei* David, 1872

Diagnosis: (1) Body size relatively large (SVL 30–120 mm, above 50 mm in most species); (2) snout rounded; (3) snout, upper eyelid and tarsal projections absent; (4) dermal folds along forearm or tarsus absent; (5) terminal phalanges of finger and toes Y-shaped; (6) skin of dorsal surfaces smooth, or scattered with small tubercles; (7) webbed fingers; (8) dorsal coloration green in most species; (9) iris without "X" shaped pattern; (10) white foam nests produced by breeding pairs; and (11) distributed in eastern Asia and northern Indochina.

Phylogenetic definition: Genus *Zhangixalus* **gen. nov.** includes species share a more recent common ancestor with *Zhangixalus dugritei* than with *Leptomantis bimaculata* and *Rhacophorus reinwardtii*.

Etymology: The generic nomen of *Zhangixalus* **gen. nov.** is named after Dr. Ya-Ping Zhang, Vice President of Chinese Academy of Sciences, for using his family name "Zhang", and *ixalus*, a common generic root for treefrogs. Dr. Zhang has contributed greatly to the promotion and development of biodiversity and evolutionary studies in China, and we acknowledge his support and encouragement to us, especially for Li's rhacophorid study. We suggest the English common name of the new genus as "Zhang's Treefrogs", and "Zhang Shu Wa Shu (张树蛙属)" in Chinese. To avoid possible confusion with regard to administration and conservation in China, we also suggest the Chinese common name of each species remains unchanged, which consistent with previous usages, e.g. *Zhangixalus dugritei* (宝兴树蛙). The gender of this genus is masculine and is named by Jia-Tang Li, Ke Jiang, Jin-Long Ren and Dechun Jiang.

Content: We currently recognized 36 species in the genus *Zhangixalus* **gen. nov.** as follows: *Z. achantharrhena* (Harvey, Pemberton, and Smith, 2002) **comb. nov.**; *Z. arboreus* (Okada and Kawano, 1924) **comb. nov.**; *Z. arvalis* (Lue, Lai, and Chen, 1995) **comb. nov.**; *Z. aurantiventris* (Lue, Lai, and Chen, 1994) **comb. nov.**; *Z. burmanus* (Andersson, 1939) **comb. nov.**; *Z. chenfui* (Liu, 1945) **comb. nov.**; *Z. dennysi* (Blanford, 1881) **comb. nov.**; *Z. dorsoviridis* (Bourret, 1937) **comb. nov.**; *Z. duboisi* (Ohler, Marquis, Swan, and Grosjean, 2000) **comb. nov.**; *Z. dugritei* (David, 1872) **comb. nov.**; *Z. dulitensis* (Boulenger, 1892) **comb. nov.**; *Z. feae* (Boulenger, 1893) **comb. nov.**; *Z. hongchibaensis* (Li, Liu, Chen, Wu, Murphy, Zhao, Wang, and Zhang, 2012) **comb. nov.**; *Z. hui* (Liu, 1945) **comb. nov.**; *Z. hungfuensis* (Liu and Hu, 1961) **comb. nov.**; *Z. jarujini* (Matsui and Panha, 2006) **comb. nov.**; *Z. leucofasciatus* (Liu and Hu, 1962) **comb. nov.**; *Z. lishuiensis* (Liu, Wang, and Jiang, 2017) **comb. nov.**; *Z. minimus* (Rao, Wilkinson, and Liu, 2006) **comb. nov.**; *Z. moltrechti* (Boulenger, 1908) **comb. nov.**; *Z. nigropunctatus* (Liu, Hu, and Yang, 1962) **comb. nov.**; *Z. omeimontis* (Stejneger, 1924) **comb. nov.**; *Z. owstoni* (Stejneger, 1907) **comb. nov.**; *Z. pinglongensis* (Mo, Chen, Liao, and Zhou, 2016) **comb. nov.**; *Z. prasinatus* (Mou, Risch, and Lue, 1983) **comb. nov.**; *Z. prominanus* (Smith, 1924) **comb. nov.**; *Z. puerensis* (He, 1999) **comb. nov.**; *Z. schlegelii* (Günther, 1858) **comb. nov.**; *Z. smaragdinus* (Blyth, 1852) **comb. nov.**; *Z. suffry* (Bordoloi, Bortamuli, and Ohler, 2007) **comb. nov.**; *Z. taipeianus* (Liang and Wang, 1978) **comb. nov.**; *Z. viridis* (Hallowell, 1861) **comb. nov.**; *Z. wui* (Li, Liu, Chen, Wu, Murphy, Zhao, Wang, and Zhang, 2012) **comb. nov.**; *Z. yaoshanensis* (Liu and Hu, 1962) **comb. nov.**; *Z. yinggelingensis* (Chou, Lau, and Chan, 2007) **comb. nov.**; *Z. zhoukaiyae* (Pan, Zhang, and Zhang, 2017) **comb. nov.**

Distribution: Occurs in southern and southwestern China mainly, as well as the southern Japan, southern slope of Himalayas, and northern part of Myanmar, Thailand, Laos, and Vietnam.

Comparison: *Zhangixalus* **gen. nov.** differs from *Rhacophorus* by the absence of dermal folds along limbs and tarsal projections (vs. present), the absence of supracloacal fold (vs. present or not); differs from *Leptomantis* by the relatively larger body size (SVL 30–120 mm, above 50 mm in most species vs. SVL 30–80 mm, within 30–50 mm in most species), rather rounded snout (vs. snout pointed), the absence of tarsal and upper eyelid projections (vs. tarsal projections, upper eyelid projections present or not), and different dorsal coloration (mostly green vs. light tan or reddish brown); differs from *Buergeria* by having "Y" shaped phalange (vs. absent); differs from *Theloderma* by relatively smooth dorsal skin (vs. dorsal surfaces with developed tubercles); differs from *Kurixalus* by the absence of prominent tubercles on outer edge of tarsus (vs. present); differs from *Nasutixalus* by the absence of a pale "X" shaped pattern on iris and raised canthus rostralis (vs. a pale "X" shaped pattern on

iris and the raised canthus rostralis present); differs from *Polypedates* by webbing between fingers (vs. no web); differs from *Taruga* by the absence of snout and tarsal projections (vs. snout projection or tarsal projections present); differs from *Chiromantis*, *Feihyla*, and *Liuixalus* by the larger body size (SVL 30–120 mm, above 50 mm in most species vs. SVL below 40 mm in most species); and differs from *Beddomixalus*, *Mercurana*, *Nyctixalus*, *Philautus*, *Pseudophilautus* and *Raochestes* by the different reproductive modes (foam nests produced by breeding pairs vs. without foam nests).

Although the taxonomic statuses of the three well-supported and highly diverged lineages of *Rhacophorus sensu lato* were preliminarily solved herein, numerous lineages within this species-rich group still remained understudied (Chan *et al*., 2018). For example, the generic placement of a further deeply divergent clade that includes *Z. achantharrhena*, *Z. dulitensis*, and *Z. prominanus* within genus *Zhangixalus* requires further study. The clade that includes *Z. achantharrhena*, *Z. dulitensis*, and *Z. prominanus* was recovered as the sister-group of all the remaining species of *Zhangixalus*, which can be diagnosed readily from latter clade in the presence of dermal folds along limbs and tarsal projections (vs. absent). The three species in this clade also differ from *Rhacophorus* and *Leptomantis* by a suit of morphological characters, including body relatively small, SVL 36–50 mm, the presence of dermal folds along limbs, well-developed supracloacal folds, the presence of tarsal projections and green dorsal coloration. However, we cannot evaluate the taxonomic status of *Z. achantharrhena*, *Z. dulitensis*, and *Z. prominanus* due to unavailable material, and tentatively assign them as members of genus *Zhangixalus*, pending further study.

Key to the genera of *Rhacophorus sensu lato*

In the absence of a key to all genera of Rhacophoridae, morphological diagnosis of some genera should be defined in the further study. Following the new taxonomic arrangement in this work, the diagnostic key to all genera of *Rhacophorus sensu lato* was provided, which including three genera, i.e. *Rhacophorus sensu stricto*, *Leptomantis*, and *Zhangixalus* **gen. nov.**

1 Dermal folds along limbs present.....*Rhacophorus*
- Dermal folds along limbs absent.....2
2 Tarsal projections absent; body size relatively moderate or large, SVL 30–120 mm (mostly above 50 mm); dorsal coloration mostly green; eastern Asia and northern Indochina distributed.....*Zhangixalus* **gen. nov.**
- Tarsal projections present or not; body size relatively small, SVL 30–80 mm (mostly within 30–50 mm); dorsal coloration mostly light tan or reddish brown; Maritime Southeast Asia distributed.....*Leptomantis*

Lastly, for the lack of both molecular and morphological data, the taxonomic status of "*Rhacophorus*" *edentulus* Müller, 1894, "*Rhacophorus*" *georgii* Roux, 1904, and "*Rhacophorus*" *turpes* Smith, 1940 remains uncertain. The unavailability of further materials for certain species hampers further taxonomic work. Possible misidentifications, undescribed new taxa, and non-monophyly of some species also reflect the need of continuous taxonomic analyses on this group (Chan *et al*., 2018).

Acknowledgements We thank Mr. Hanren LIU and Ms. Tong YANG for their kind helps in the molecular data collection; Dr. Robert W. MURPHY for polishing English of the manuscript; and Mr. Cheng LI for photos. This work was supported by National Key R&D Program of China (2016YFC1200705); the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB31000000); the National Natural Science Foundation of China (31722049, 31772434); Key Research Program of Frontier Sciences, CAS (QYZDB-SSW-SMC058); the Youth Innovation Promotion Association of CAS; Southeast Asia Biodiversity Research Institute (Y4ZK111B01); and the CAS "Light of West China" Program (2018XBZG_JCTD_001).

References

Abraham R. K., Pyron R. A., Ansil B. R., Zachariah A., Zachariah A. 2013. Two novel genera and one new species of treefrog (Anura: Rhacophoridae) highlight cryptic diversity in the Western Ghats of India. Zootaxa, 36(20): 177–199

Ahl E. 1927. Zur Systematik der asiatischen Arten der Froschgattung *Rhacophorus*. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1927: 35–47

Ahl E. 1931. Amphibia: Anura III (Polypedatidae). Das Tierreich, 477

AmphibiaChina. 2018. The database of Chinese amphibians. Retrieved from http://www.amphibiachina.org/. Accessed 30 March 2018

Anderson J. 1871. A list of the reptilian accession to the Indian Museum, Calcutta from 1865 to 1870, with a description of some new species. J Asiatic Soc Bengal, 40(2): 12–39

Andersson L. G. 1939 "1938". Batrachians from Burma collected by Dr. R. Malaise, and from Bolivia and Ecuador collected by Dr. C. Hammarlund. Arkiv för Zool, 30(23): 1–24

Biju S. D., Shouche Y. S., Dubois A., Dutta S. K., Bossuyt F. 2010. A ground-dwelling rhacophorid frog from the highest mountain peak of the Western Ghats of India. Curr Sci, 98: 1119–1125

Biju S., Kamei R. G., Mahony S., Thomas A., Garg S., Sircar G., Suyesh R. 2013. Taxonomic review of the tree frog genus *Rhacophorus* from the Western Ghats, India (Anura: Rhacophoridae), with description of ontogenetic colour changes and reproductive behaviour. Zootaxa, 3636(2): 257–289

Blanford W. T. 1881. On a collection of reptiles and frogs chiefly from Singapore. P Zool Soc Lond, 49(1): 215–226

Blyth E. 1852. Report of Curator, Zoological Department. J Asiatic Soc Bengal, 21: 341–358

Bordoloi S., Bortamuli T., Ohler A. 2007. Systematics of the genus *Rhacophorus* (Amphibia, Anura): identity of red-webbed forms and description of a new species from Assam. Zootaxa, 1653(1): 1–20

Boulenger, G. A. 1882. Description of a new genus and species of frogs of the family Ranidae. Ann Mag Nat Hist, 5(10): 35

Boulenger G. A. 1883. Description of new species of reptiles and batrachians in the British Museum. Ann Mag Nat Hist, 12(69): 161–167

Boulenger G. A. 1892. An account of the reptiles and batrachians collected by Mr. C. Hose on Mt. Dulit, Borneo. P Zool Soc Lond, 1982: 505–508

Boulenger G. A. 1893. Concluding report on the reptiles and batrachians obtained in Burma by Signor L. Fea dealing with the collection made in Pegu and the Karin Hills in 1887–1888 Annali del Museo Civico di Storia Naturale di Genova, 13: 304–347

Boulenger G. A. 1895. Descriptions of four new batrachians discovered by Mr. Charles Hose in Borneo. Ann Mag Nat Hist, 16(92): 169–173

Boulenger G. A. 1896. Descriptions of new reptiles and batrachians collected in Celebes by Drs. P. and F. Sarasin. J Nat Hist, 17(101): 393–395

Boulenger G. A. 1903. Report on the batrachians and reptiles. Annandale, N., and H. C. Robinsoneds., Fasciculi Malayenses. Anthropological and Zoological Results of an Expedition to Perak and the Siamese Malay States 1901–1903 undertaken by Nelson Annandale and Herbert C. Robinson under the auspecies of the University of Edinburgh and the University of Liverpool. Zoology, 2: 131–176

Boulenger G. A. 1908. Descriptions of a new frog and a new snake from Formosa. Ann Mag Nat Hist, 2(8): 221–222

Boulenger G. A. 1920. Reptiles and batrachians collected in Korinchi, West Sumatra, by Messrs. H.C. Robinson and C. Boden Kloss. J Federated Malay States Mus, 8: 285–306

Bourret R. 1937. Notes herpétologiques sur l'Indochine française. XIV. Les batraciens de la collection du Laboratoire des Sciences Naturelles de l'Université. Descriptions de quinze especes ou variétés nouvelles. Annexe au Bulletin Général de l'Instruction Publique, 1937: 5–56

Chan K. O., Grismer L. L. 2010. Re-assessment of the Reinwardt's Gliding Frog, *Rhacophorus reinwardtii* (Schlegel 1840) (Anura: Rhacophoridae) in southern Thailand and peninsular Malaysia and its re-description as a new species. Zootaxa, 2505: 40–50

Chan K. O., Grismer L. L., Brown R. M. 2018. Comprehensive multi-locus phylogeny of Old World tree frogs (Anura: Rhacophoridae) reveals taxonomic uncertainties and potential cases of over- and underestimation of species diversity. Mol Phylogenet Evol (Online)

Chou W. H., Lau M. W. N., Chan B. P. L. 2007. A new treefrog of the genus *Rhacophorus* (Anura: Rhacophoridae) from Hainan Island, China. Raffles Bull Zool, 55(1): 157–165

Das I., Haas A. 2005. A new species of *Rhacophorus* (Anura: Rhacophoridae) from Gunung Gading, Sarawak. Raffles Bull Zool, 53(2): 257–263

David A. 1872 "1871". Rapport adressé a MM. les Professeurs-Administráteurs du Museum d'histoire naturelle. Nouvelles Archives du Muséum d'Histoire Naturelle, 7: 75–100

Dehling J. M. 2008. A new treefrog (Anura: Rhacophoridae: *Rhacophorus*) from Gunung Mulu, Borneo. Salamandra, 44(4): 193–205

Dehling J. M. 2011. Taxonomic status of the population of *Rhacophorus angulirostris* Ahl, 1927 (Anura: Rhacophoridae) from Sumatera Barat (West Sumatra) and its description as a new species. Salamandra, 47(3): 133–143

Dehling J. M. 2015. A new species of *Rhacophorus* (Anura: Rhacophoridae) from Gunung Kinabalu, Borneo. Salamandra, 51(1): 1–11

Dehling J. M., Grafe T. U. 2008. A new treefrog of the genus *Rhacophorus* (Anura: Rhacophoridae) from Brunei Darussalam (Borneo). Salamandra, 44(2): 101–112

Dubois A. 1987. Miscellanea taxinomica batrachologica (I). Alytes, 6(1): 1–9

Fei L., Hu S. Q., Ye C. Y., Huang Y. 2009. Fauna Sinica. Amphibia. Vol.2. Anura., Beijing: Science Press, 957 pp (In Chinese)

Fei L., Hu S. Q., Ye C. Y., Wu G. F. 1977. A survey of amphibians in Xizang (Tibet). Acta Zool Sinica, 23(1): 54–63

Fei L., Ye C. Y., Jiang J. P. 2012. Colored Atlas of Chinese Amphibians and Their Distributions. Sichuan, China: Sichuan Publishing House of Science & Technology, 619 pp (In Chinese)

Frost D. R. 2018. Amphibian Species of the World: an Online Reference. Version 6.0. Retrieved from http://research.amnh.org/herpetology/amphibia/index.html. Accessed 30 March 2018

Günther A. C. L. G. 1858. Neue Batrachier in der Sammlung des britischen Museums. Archiv für Naturgeschichte, 24: 319–328

Hallowell E. 1861 "1860". Report upon the Reptilia of the North Pacific Exploring Expedition, under command of Capt. John Rogers, U. S. N. P Acad Nat Sci Phila, 12: 480–510

Hamidy A., Kurniati H. 2015. A new species of tree frog genus *Rhacophorus* from Sumatra, Indonesia (Amphibia, Anura). Zootaxa, 3947(1): 49–66

Harvey M. B., Pemberton A. J., Smith E. N. 2002. New and poorly known parachuting frogs (Rhacophoridae: *Rhacophorus*) from Sumatra and Java. Herpetol Monogr, 16(1): 46–92

He X. R. 1999. A new species of the family Rhacophoridae from Yunnan—*Polypedates puerensis*. Sichuan J Zool, 18(3): 99–100

Hertwig S. T., Das I., Schweizer M., Brown R., Haas A. 2012. Phylogenetic relationships of the *Rhacophorus everetti* - group and implications for the evolution of reproductive modes in *Philautus* (Amphibia: Anura: Rhacophoridae). Zool Scr, 41(1):

29–46

Huang Y. Z. 1983. A new species of flying frog from Xizang—*Rhacophorus verrucopus*. Acta Herpetol Sinica, 2(4): 63–65

Inger R. F. 1954. On a collection of amphibians from Mount Kina Balu, North Borneo. J Wash Acad Sci, 44(8): 250–251

Inger R. F. 1954. Systematics and zoogeography of Philippine Amphibia. Fieldiana Zool, 33: 181–531

Inger R. F. 1966. The systematics and zoogeography of the Amphibia of Borneo. Fieldiana Zool, 52(2): 1–402

Inger R. F. 1999. Frogs of Vietnam: a report on new collections. Fieldiana Zool New Ser, 92: 1–46

Inger R. F., Haile N. S. 1959. Two new frogs from Sarawak. Sarawak Mus J, 9: 270–276

Inger R. F., Orlov N. L., Darevsky I. S. 1999. Frogs of Vietnam: A report on new collections. Fieldiana Zool, 92: 1–46

Iskandar D. T., Colijn E. 2000. Preliminary Checklist of Southeast Asian and New Guinean Herpetofauna: Amphibians. Treubia, 31: 1–133

Jerdon T. C. 1870. Notes on Indian herpetology. P Asiatic Soc Bengal, 1870: 66–85

Jiang K., Yan F., Wang K., Zou D. H., Li C., Che J. 2016. A new genus and species of treefrog from Medog, southeastern Tibet, China (Anura, Rhacophoridae). Zool Res, 37(1): 15–20

Kuhl H., Van Hasselt J. C. 1822. Uittreksels uit breieven van de Heeren Kuhl en van Hasselt, aan de Heeren C. J. Temminck, Th. van Swinderen en W. de Haan. Algemeene Konst-en Letter-Bode, 7: 99–104

Lanfear R., Calcott B., Ho S. Y., Guindon S. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol Biol Evol, 29(6): 1695–1701

Li J. T., Che J., Bain R. H., Zhao E. M., Zhang Y. P. 2008. Molecular phylogeny of rhacophoridae (anura): a framework of taxonomic reassignment of species within the genera aquixalus, chiromantis, rhacophorus, and philautus. Mol Phylogenet Evol, 48(1): 302–312

Li J. T., Che J., Murphy R. W., Zhao H., Zhao E. M., Rao D. Q., Zhang Y. P. 2009. New insights to the molecular phylogenetics and generic assessment in the Rhacophoridae (Amphibia: Anura) based on five nuclear and three mitochondrial genes, with comments on the evolution of reproduction. Mol Phylogenet Evol, 53(2): 509–522

Li J. T., Li Y., Klaus S., Rao D. Q., Hillis, D M., Zhang Y. P. 2013. Diversification of Rhacophorid frogs provides evidence for accelerated faunal exchange between India and Eurasia during the Oligocene. P Natl Acad Sci USA, 110(9): 3441

Li J. T., Li Y., Murphy R. W., Rao D. Q., Zhang Y. P. 2012. Phylogenetic resolution and systematics of the Asian tree frogs, *Rhacophorus* (Rhacophoridae, Amphibia). Zool Scr, 41(6): 557–570

Li J. T., Liu J., Chen Y. Y., Wu J. W., Murphy R. W., Zhao E. M., Wang Y. Z., Zhang Y. P. 2012. Molecular phylogeny of treefrogs in the *Rhacophorus dugritei* species complex (Anura: Rhacophoridae), with descriptions of two new species. Zool J Linn Soc, 165(1): 143–162

Liang Y. S., Wang C. S. 1978. A new tree frog *Rhacophorus taipeianus* (Anura: Rhacophoridae) from Taiwan (Formosa). Quart J Taiwan Mus, 31: 185–202

Liu B. Q., Wang Y. F., Jiang K., Chen H. M., Xu J. N., Wu C. H. 2017. A new species of the genus *Rhacophorus* found in Zhejiang, China (Anura: Rhacophoridae). Chin J Zool, 52(3): 361–372

Liu C. C. 1945. New frogs from West China. J West China Border Res Soc, 15: 28–44

Liu C. C., Hu S. Q. 1960 "1959". Preliminary report of Amphibia from southern Yunnan. Acta Zool Sinica, 11(4): 508–538

Liu C. C., Hu S. Q. 1961. Tailless Amphibians of China, Beijing: Science Press

Liu C. C., Hu S. Q. 1962. A herpetological report of Kwangsi. Acta Zool Sinica, 14: 73–104

Liu C. C., Hu S. Q., Yang F. H. 1962. Preliminary report of Amphibia from western Kweichow. Acta Zool Sinica, 14(3): 381–392

Lue K. Y., Lai J. S., Chen S. L. 1994. A new species of *Rhacophorus* (Anura: Rhacophoridae) from Taiwan. Herpetologica, 50: 303–308

Lue K. Y., Lai J. S., Chen S. L. 1995. A new species of *Rhacophorus* (Anura: Rhacophoridae) from Taiwan. J Herpetol, 29: 338–345

Malkmus R., Brühl C. 2002. Amphibians & Reptiles of Mount Kinabalu (North Borneo). ARG Gantner Ruggell, 1–424

Manthey U., Steiof C. 1998. *Rhacophorus cyanopunctatus* sp. n. (Anura: Rhacophoridae), ein neuer Flugfrosch von der Malaiischen Habinsel, Sumatra und Borneo. Sauria, 20: 37–42

Mathew R., Sen N. 2009. Studies on little known amphibians of Northeast India. Rec Zool Surv India, 293: 1–64

Matsui M., Panha S. 2006. A new species of *Rhacophorus* from eastern Thailand (Anura: Rhacophoridae). Zool Sci, 23(5): 477–481

Matsui M., Shimada T., Sudin A. 2013. A new gliding frog of the genus *Rhacophorus* from Borneo. Curr Herpetol, 32(2): 112–124

Meegaskumbura M., Meegaskumbura S., Bowatte G., Manamendra-Arachchi K., Pethiyagoda R., Hanken J., Schneider C. J. 2010. *Taruga* (Anura: Rhacophoridae), a new genus of foam-nesting tree frogs endemic to Sri Lanka. Ceylon Journal of Science. Bio Sci, 39: 75–94

Mo Y. M., Chen W. C., Liao X., Zhou S. C. 2016. A new species of the genus *Rhacophorus* (Anura: Rhacophoridae) from southern China. Asian Herpetol Res, 7(3): 139–150

Mo Y. M., Jiang J. P., Xie F., Ohler A. 2008. A new species of *Rhacophorus* (Anura: Ranidae) from China. Asiatic Herpetol Res, 11: 85–92

Mou Y. P., Risch J. P., Lue K. Y. 1983. *Rhacophorus prasinatus*, a new tree frog from Taiwan, China (Amphibia, Anura, Rhacophoridae). Alytes, 2: 154–162

Müller F. 1894. Reptilien und Amphibien aus Celebes. Verhandlungen der Naturforschenden Gesellschaft in Basel, 10: 825–843

Nguyen T. T., Pham C. T., Nguyen T. Q., Ninh H. T., Ziegler T. 2017. A new species of *Rhacophorus* (Amphibia: Anura: Rhacophoridae) from Vietnam. Asian Herpetol Res, 8(4): 221–234

O'Connell K. A., Smart U., Smith E. N., Hamidy A., Kurniawan N., Fujita M. K. 2018. Within–island

diversification underlies parachuting frog (*Rhacophorus*) species accumulation on the Sunda shelf. J Biogeogr (Online)

Ohler A., Delorme M. 2006. Well known does not mean well studied: morphological and molecular support for existence of sibling species in the Javanese gliding frog *Rhacophorus reinwardtii* (Amphibia, Anura). C R Biologies, 329(2): 86–97

Ohler A., Deuti K. 2018. *Polypedates smaragdinus* Blyth, 1852-a senior subjective synonym of *Rhacophorus maximus* Günther, 1858. Zootaxa, 4375(2): 273–280

Ohler A., Marquis O., Swan S. R., Grosjean S. 2000. Amphibian biodiversity of Hoang Lien Nature Reserve (Lao Cai Province, northern Vietnam) with description of two new species. Herpetozoa, 13: 71–87

Okada Y., Kawano U. 1924. On the ecological distribution of two new varieties of *Rhacophorus* in Japan. Zool Mag, 36: 144–153

Onn C. K., Ahmad N. 2009. Distribution and natural history notes on some poorly known frogs and snakes from Peninsular Malaysia. Herpetol Rev, 40(3): 294–301

Orlov N. L. 2008. Description of a new species of *Rhacophorus* genus (Amphibia: Anura: Rhacophoridae) from Kon Cha Rang area (Gia Lai Province, Vietnam). Russ J Herpetol, 15: 133–140

Orlov N. L., Gnophanxay S., Phimminith T., Phomphoumy K. 2010 "2009". A new species of *Rhacophorus* Genus (Amphibia: Anura: Rhacophoridae: Rhacophorinae) from Khammouan Province, Lao PDR. Russ J Herpetol, 16(4): 295–303

Orlov N. L., Lathrop A., Murphy R. W., Ho T. C. 2001. Frogs of the family Rhacophoridae (Anura: Amphibia) in the northern Hoang Lien Mountains (Mount Fan Si Pan, Sa Pa District, Lao Cai Province), Vietnam. Russ J Herpetol, 8(1): 17–44

Orlov N. L., Nguyen N. S., Ho T. C. 2008. Description of a new species and new records of *Rhacophorus* genus (Amphibia: Anura: Rhacophoridae) with the review of amphibians and reptiles diversity of Ghu Yang Sin National Park (Dac Lac Province, Vietnam). Russ J Herpetol, 15(1): 67–84

Orlov N. L., Poyarkov N. A., Vassilieva A. B., Ananjeva N. B., Nguyen T. T., Sang N. V., Geissler P. 2012. Taxonomic notes on rhacophorid frogs (Rhacophorinae: Rhacophoridae: Anura) of southern part of Annamite Mountains (Truong Son, Vietnam), with description of three new species. Russ J Herpetol, 19(1): 23–64

Ostroshabov A. A., Orlov N. L., Nguyen T. T. 2013. Taxonomy of frogs of genus *Rhacophorus* of "*hoanglienensis–orlovi*" complex. Russ J Herpetol, 20(4): 301–324

Pan T., Zhang Y. N., Wang H., Wu J., Kang X., Qian L. F., Li K., Zhang Y., Chen J. Y., Rao D. Q., Jiang J. P., Zhang B. W. 2017. A New Species of the Genus *Rhacophorus* (Anura: Rhacophoridae) from Dabie Mountains in East China. Asian Herpetol Res, 8(1): 1–13

Pan T., Zhang Y., Wang H., Wu J., Kang X., Qian L., Chen J., Rao D., Jiang J., Zhang B. 2017. The reanalysis of biogeography of the Asian tree frog, *Rhacophorus* (Anura: Rhacophoridae): geographic shifts and climatic change influenced the dispersal process and diversification. Peer J, 5(11): e3995

Peters W. C. H. 1867. Herpetologische notizen. Monatsberichte der königlich Akademie der Wissenschaften zu Berlin, 1867: 13–37

Rambaut A., Suchard M., Xie D., Drummond A. 2013. Tracer, version 1.6, MCMC trace analysis package. Retrieved from http://tree.bio.ed.ac.uk/software/tracer/ Accessed 7 March 2018

Rao D. Q., Wilkinson J. A., Liu H. N. 2006. A new species of *Rhacophorus* (Anura: Rhacophoridae) from Guangxi Province, China. Zootaxa, 1258: 17–31

Ronquist F., Teslenko M., Mark P. V. D., Ayres D. L., Darling A., Hohna S., Larget B., Liu L., Suchard M. A., Huelsenbeck J. P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol, 61(3): 539–542

Roux J. 1904. Reptilien und Amphibien aus Celebes. Verhandlungen der Naturforschenden Gesellschaft in Basel, 15(3): 425–433

Rowley J. J. L., Le D. T. T., Thi D. A., Stuart B. L., Hoang H. D. 2010. A new frog of the genus *Rhacophorus* (Anura: Rhacophoridae) from southern Vietnam. Zootaxa, 1(2727): 45–55

Rowley J. J. L., Tran D. T. A., Hoang H. D., Le D. T. T. 2012. A new large species of large Flying Frog (Rhacophoridae: *Rhacophorus*) from lowland forests of southern Vietnam. J Herpetol, 46(4): 480–487

Schlegel H. 1837. Abbildungen neuer oder unvollständig bekannter Amphibien, nach der Natur oder dem Leben entworfen, herausgegeben und mit einem erläuternden Texte begleitet. Düsseldorf: Arnz & Co

Schlegel H. 1840. Abbildungen neuer oder unvollständig bekannter Amphibien, nach der Natur oder dem Leben entworfen, herausgegeben und mit einem erläuternden. Atlas. Düsseldorf: Arnz & Co

Smith M. A. 1924. New tree-frogs from Indo-China and the Malay Peninsula. P Zool Soc Lond, 94(1): 225–234

Smith M. A. 1924. Two lizards and a new tree frog from the Malay Peninsula. J Federated Malay States Mus, 11: 183–186

Smith M. A. 1940. The amphibians and reptiles obtained by Mr. Ronald Kaulback in Upper Burma. Rec Indian Mus, 42: 465–486

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models, v. 7.03. Bioinformatics, 22: 2688–2690.

Stejneger L. 1907. Herpetology of Japan and adjacent territory. Bull U S Nat Mus, 58: xx + 577

Stejneger L. 1924. Herpetological novelties from China. Occasional Papers Boston Soc Nat Hist, 5: 119–121

Streicher J. W., Hamidy A., Harvey M. B., Anders B., Shaney K. J., Kurniawan N., Smith E. N. 2014. Mitochondrial DNA reveals a new species of parachuting frog (Rhacophoridae: *Rhacophorus*) from Sumatra. Zootaxa, 3878(4): 351–365

Sun Y. B. 2017. FasParser: a package for manipulating sequence data. Zool Res, 38(2): 110–112

Van Kampen P. N. 1923. The Amphibia of the Indo-Australian Archipelago. Leiden: E. J. Brill Ltd, 1–31

Vasudevan K., Dutta S. K. 2000. A new species of *Rhacophorus* (Anura: Rhacophoridae) from the Western Ghats, India. Hamadryad, 25: 21–38

Yang T. 2018. Molecular Phylogenetics, Biogeography and

Evolution of *Rhacophorus* (Rhacophoridae: Amphibia). Chengdu: Chengdu Institute of Biology, Chinese Academy of Sciences

Ziegler T., Köhler J. 2001. *Rhacophorus orlovi* sp. n., ein neuer Ruderfrosch aus Vietnam (Amphibia: Anura: Rhacophoridae). Sauria. Berlin, 23: 37–46

Appendix

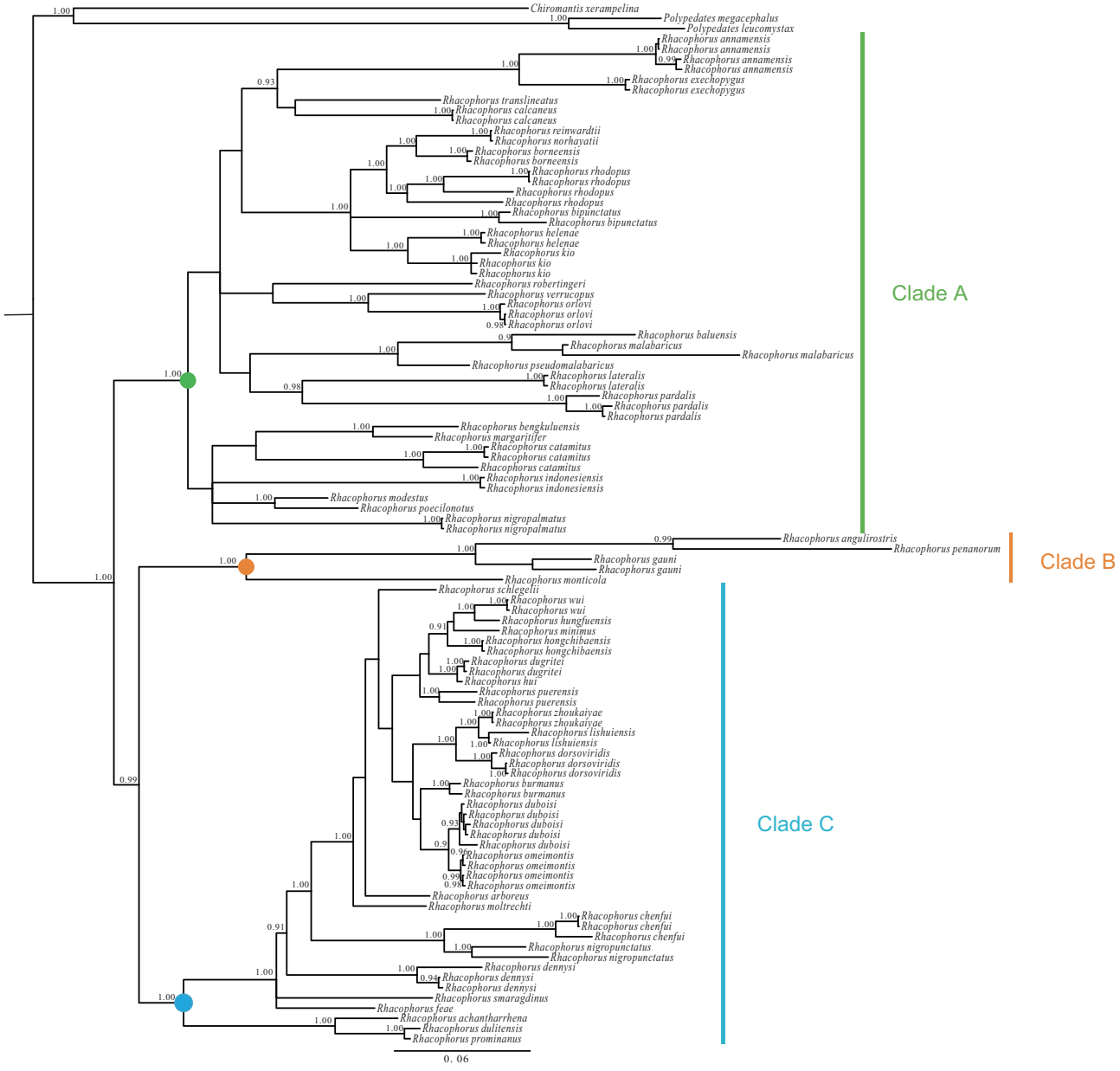

Figure S1 Bayesian phylogenetic relationships of species of *Rhacophorus*, based on three mitochondrial genes: 12S rRNA, tRNA-val and 16S rRNA. Circles on nodes correspond to three clades: Clade A (green), Clade B (orange), Clade C (blue). Numbers beside the nodes are given as Bayesian posterior probabilities (BPP) (≥0.90 retained).

Table S1 Samples, with sampling site, museum voucher nos., and GenBank accession Nos. of corresponding sequences. "-" represents missing data.

Taxon	Locality	Voucher Number	GenBank accession Nos.
Chiromantis xerampelina	-	CAS uncatalogued	AF458132
Polypedates leucomystax	Myanmar: Chatthin	USNM GZ 33881	AB728168
Polypedates megacephalus	-	MM Pm	AF458141
Rhacophorus achantharrhena	Indonesia: Sumatra	ENS 14757	KX398867
Rhacophorus angulirostris	-	GenBank	AF215360
Rhacophorus annamensis	Vietnam	AMNH A161414	DQ283047
Rhacophorus annamensis	Vietnam	FMNH 253934	GQ204768
Rhacophorus annamensis	Vietnam: Ta Kou Mountain Natural Reserve	KIZ 1196	JX219446
Rhacophorus annamensis	Vietnam: Bu Gia Map National Park	KIZ 64	JX219448
Rhacophorus arboreus	Japan	TTU-R-11748	AF458142
Rhacophorus baluensis	Malaysia: Sabah	FM235958	KC961239
Rhacophorus bengkuluensis	Indonesia: Sumatra, Lampung	UTA A-62770	KM212948
Rhacophorus bipunctatus	Myanmar: Bee Hoe village, Chin State	CAS 235303	JX219444
Rhacophorus bipunctatus	Myanmar: Putao District, Kachin State	CAS 229913	JX219445
Rhacophorus borneensis	Malaysia: Sabah, Maliau Basin	BORN:22410	AB781693
Rhacophorus borneensis	Malaysia: Sabah, Maliau Basin	BORN:22411	AB781694
Rhacophorus burmanus	China: Mt. Gaoligong, Yunnan	SCUM 060614L	EU215537
Rhacophorus burmanus	China: Motuo, Xizang	RAO 6239	JX219422
Rhacophorus calcaneus	Vietnam: Bi Doup National Park	KIZ 528	JX219450
Rhacophorus calcaneus	Vietnam: Bi Doup National Park	KIZ 746	JX219451
Rhacophorus catamitus	Indonesia	ENS 7657	JF748387
Rhacophorus catamitus	Indonesia	ENS 7662	JF748388
Rhacophorus catamitus	Indonesia: Sumatra	ENS 14726	KX398877
Rhacophorus chenfui	China: Mt. Omei, Sichuan	SCUM 060404L	EU215534
Rhacophorus chenfui	China: Zhaotong, Yunnan	RAO ZT 0806013	JX219431
Rhacophorus chenfui	China: Mt. Omei, Sichuan	Li 05	JX219432
Rhacophorus dennysi	Vietnam	MNHN 1440K	AY880611
Rhacophorus dennysi	China: Shaoguan, Guangdong	SCUM 060401L	EU215545
Rhacophorus dennysi	China: Taoyuan, Hunan	Li06	JX219433
Rhacophorus dorsoviridis	Vietnam: Sa Pa, Lao Cai	ROM38015	JX219423
Rhacophorus dorsoviridis	China: Jinping, Yunnan	RAO060821200	JX219424
Rhacophorus dorsoviridis	China: Pingbian, Yunnan	YN080446	JX219425
Rhacophorus duboisi	China: Mt. Dawei, Yunnan	SCUM 061104L	EU215536
Rhacophorus duboisi	China: Jinxiu, Guangxi	RAOYN080492	JX219412
Rhacophorus duboisi	Vietnam: Sa Pa, Lao Cai	ROM 38771	JX219413
Rhacophorus duboisi	Vietnam: Sa Pa, Lao Cai	ROM 38758	JX219414
Rhacophorus duboisi	China: Jinping, Yunnan	RAOL060821289	JX219415
Rhacophorus dugritei	China: Hongya, Sichuan	SCUM 051017L	EU215540
Rhacophorus dugritei	China: Baoxing, Sichuan	SCUM 051001L	EU215541
Rhacophorus dulitensis	Malaysia	RAO081201	JX219434
Rhacophorus exechopygus	Vietnam	RH 06085	GQ469980

(Continud Table S1)

Taxon	Locality	Voucher Number	GenBank accession Nos.
Rhacophorus exechopygus	Vietnam: Gia Lai	VNMN:4107	LC010585
Rhacophorus feae	China: Hekou, Yunnnan	SCUM 050642WXJ	EU215544
Rhacophorus gauni	-	GenBank	AF215362
Rhacophorus gauni	Malaysia: Sarawak, Bintulu Division	FMNH273928	JX219456
Rhacophorus helenae	Vietnam	UNS:00451	JQ288090
Rhacophorus helenae	Vietnam	ZFMK:92544	JQ288091
Rhacophorus hongchibaensis	China:Wuxi, Chongqing	CIB 097696	JN688882
Rhacophorus hongchibaensis	China:Wuxi, Chongqing	CIB 097687	JN688883
Rhacophorus hui	China: Zhaojue, Sichuan	Li01	JN688878
Rhacophorus hungfuensis	China: Wenchuan, Sichuan	SCUM 060425L	EU215538
Rhacophorus indonesiensis	Indonesia	MZB:Amp:23619	AB983367
Rhacophorus indonesiensis	Indonesia	MZB:Amp:23626	AB983368
Rhacophorus kio	Vietnam	Genbank	AF215188
Rhacophorus kio	Vietnam	Genbank	AF458147
Rhacophorus kio	China: Xishuangbanna, Yunnan	SCUM 37941C	EU215532
Rhacophorus lateralis	India:Mudigere	RBRL 050709-35, 36, 37	AB530548
Rhacophorus lateralis	India: Bygoor, Karnataka	SDB.2010.330	KC571277
Rhacophorus lishuiensis	China: Lishui, Zhejiang	YPX52658	KY653717
Rhacophorus lishuiensis	China: Lishui, Zhejiang	YPX47791	KY653718
Rhacophorus malabaricus	India: Madikeri	GenBank	AB530549
Rhacophorus malabaricus	India	GenBank	DQ346957
Rhacophorus margaritife	Indonesia: Java	ENS 16162	KX398889
Rhacophorus minimus	China: Mt. Dayao, Guangxi	KIZ 061214YP	EU215539
Rhacophorus modestus	Indonesia: Sumatra	ENS 16853	KX398904
Rhacophorus moltrechti	China: Lianhuachi, Taiwan	SCUM 061106L	EU215543
Rhacophorus monticola	Indonesia: Sulawesi	RMB 1236	AY326060
Rhacophorus nigropalmatus	Malaysia	Genbank	JX219437
Rhacophorus nigropalmatus	Malaysia	RAO081203	JX219438
Rhacophorus nigropunctatus	China: Longling, Yunnan	RAO 3496	JX219428
Rhacophorus nigropunctatus	China: Weining, Guizhou	GZ 070658	JX219430
Rhacophorus norhayatii	Malaysia: Johor, Endau Rompin	NNRn	AB728191
Rhacophorus omeimontis	China: Pengxian, Sichuan	SCUM 0606137L	EU215535
Rhacophorus omeimontis	China: Zhanotong, Yunnan	ZT 0806010	JX219419
Rhacophorus omeimontis	China: Yaan, Sichuan	Li 02	JX219420
Rhacophorus omeimontis	China: Mt. Omei, Sichuan	SC 080505	JX219421
Rhacophorus orlovi	Vietnam	AMNH A161405	DQ283049
Rhacophorus orlovi	China: Maguan, Yunan	RAO 03309	JX219435
Rhacophorus orlovi	China: Maguan, Yunan	LJT R44	KC465840
Rhacophorus pardalis	Malaysia: Kota Marudu District, Sabah	FMNH 235741	JX219452
Rhacophorus pardalis	Malaysia	FMNH 231366	JX219453
Rhacophorus pardalis	Malaysia: Bintulu Division, Sarawak	FMNH 273243	JX219454
Rhacophorus penanorum	Malaysia: Sarawak	ZRC 1.12116	JN377350

(Continud Table S1)

Taxon	Locality	Voucher Number	GenBank accession Nos.
Rhacophorus poecilonotus	Indonesia: Sumatra	ENS 16480	KX398920
Rhacophorus prominanus	Indonesia: Sumatra	ENS 16994	KX398925
Rhacophorus pseudomalabaricus	India: Kadalar, Kerala	SDB.2011.1010	KC593855
Rhacophorus puerensis	China: Puer, Yunnan	SCUM 060649L	EU215542
Rhacophorus puerensis	Vietnam: Sa Pa, Lao Cai	ROM 37996	JN688891
Rhacophorus reinwardtii	Malaysia	Rao081205	JX219443
Rhacophorus rhodopus	China: Mengyang, Jinghong	SCUM 060692L	EU215531
Rhacophorus rhodopus	China: Longchuan, Yunnan	Loc 08007018	JX219439
Rhacophorus rhodopus	China: Lvchun, Yunnan	Lc0805109	JX219440
Rhacophorus rhodopus	China: Motuo, Xizang	RAO 06245	JX219441
Rhacophorus robertingeri	Vietnam: Gig Lai	VNMN:4123	LC010613
Rhacophorus schlegelii	Japan	KUHE 26251	AY880615
Rhacophorus smaragdinus	China: Motuo, Xizang	RAO 6241	JX219411
Rhacophorus translineatus	China: Motuo, Xizang	RAO 6237	JX219449
Rhacophorus verrucopus	China: Motuo, Xizang	6254 RAO	JX219436
Rhacophorus wui	China: Lichuan, Hubei	CIB 097690	JN688880
Rhacophorus wui	China: Lichuan, Hubei	CIB 097685	JN688881
Rhacophorus zhoukaiyae	China: Dabie Mountains, Anhui	AHU-RhaDb-150418-02	KU601494
Rhacophorus zhoukaiyae	China: Dabie Mountains, Anhui	AHU-RhaDb-150418-03	KU601495